Life cycle, habitat selection and home ranges of *Arctosa cinerea* (Fabricius, 1777) (Araneae: Lycosidae) in a braided section of the Upper Isar (Germany, Bavaria)

Volker FRAMENAU[1, 2], Martin DIETERICH[2], Michael REICH[2]
& Harald PLACHTER[2]
[1] University of Melbourne
   Department of Zoology, Parkville, Victoria 3052, Australia;
[2] Universität Marburg
   Fachbereich Biologie, Fachgebiet Naturschutz, D-35032 Marburg, Germany.

Life cycle, habitat selection and home ranges of *Arctosa cinerea* **(Fabricius, 1777) (Araneae: Lycosidae) in a braided section of the Upper Isar (Germany, Bavaria).** - Investigations on basic population characters of the lycosid spider *Arctosa cinerea* were conducted from June 1994 to July 1995. The spiders were individually marked and recaptured to estimate abundance and home range size. Maximum spider densities found were 0,3 ind./m^{2}. During their larval stages and during the first four weeks as adults, the spiders prefer gravelbanks where they hide under stones during the day. As they get older they prefer sandy substrates for the establishment of their burrows. *A. cinerea* has a two year life cycle. The species is diplochronous with reproductive periods in autumn and spring. The adult sex ratio is biased towards females (1 : 1,8). Maximum home ranges were 1.260 m[2] for males and 1.140 m[2] for females.

Key-words: Lycosidae - *Arctosa cinerea* - life cycle - sex ratio - habitat selection - home range - river - floodplains.

INTRODUCTION

The floodplains of braided alpine rivers provide a highly dynamic habitat. Recurring flood events often produce gravel banks bare of any vegetation. These are inhabited by a specifically adapted arthropod community, characterized by a large number of predators. Particularly ground beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Araneae) are abundant on gravel bars (KÜHNELT 1943, PLACHTER 1986a, b, HERING 1996, MANDERBACH & REICH 1996). As there are no vertical structures to fix a web, the spider community on the gravel bars mainly consists of ground living species. Most abundant are lycosid and linyphiid spiders (e.g. BOUMEZZOUGH 1983, BIGOT & FAVET 1985, DRÖSCHMEISTER 1994).

One of the riparian inhabitants, the lycosid spider *Arctosa cinerea* (Fabricius, 1777), can be found in the whole palaearctic region (PLATNICK 1993). *A. cinerea* is up to 20 mm in size and therefore one of the largest predacious arthropods on alpine gravel banks and one of the largest spiders in Central Europe.

A. cinerea not only occurs on riverbeds and lakesides, but also on sandy beaches and coastal dunes, where the spiders construct burrows to hibernate and to breed. In Germany, A. cinerea has also been found in gravel pits (SACHER 1992).

Stochasticity, either demographic, environmental or catastrophical, plays a major role for the population dynamics of most species and for the development of certain ecosystems (EWENS *et al.* 1987, SHAFFER 1987, REICE 1994). Local extinction of populations is one of the characteristics in such ecosystems (LUKEN 1990, HOVESTADT *et al.* 1992). Braided floodplains are characterised by floods, which mainly occur during the later spring in Central Europe. The aim of this study is to demonstrate how life cycle and habitat association of *A. cinerea* are adapted to recurring flood events and what spatial needs *A. cinerea* has within its habitat (home range size).

STUDY AREA AND METHODS

The study site (fig. 1) was located in the braided floodplain of the Upper Isar (Germany, Southern Bavaria) between Wallgau and the Sylvenstein Reservoir. The floodplain is between 300 and 500 m wide and the Isar has a slope of 5-6 ‰. Since
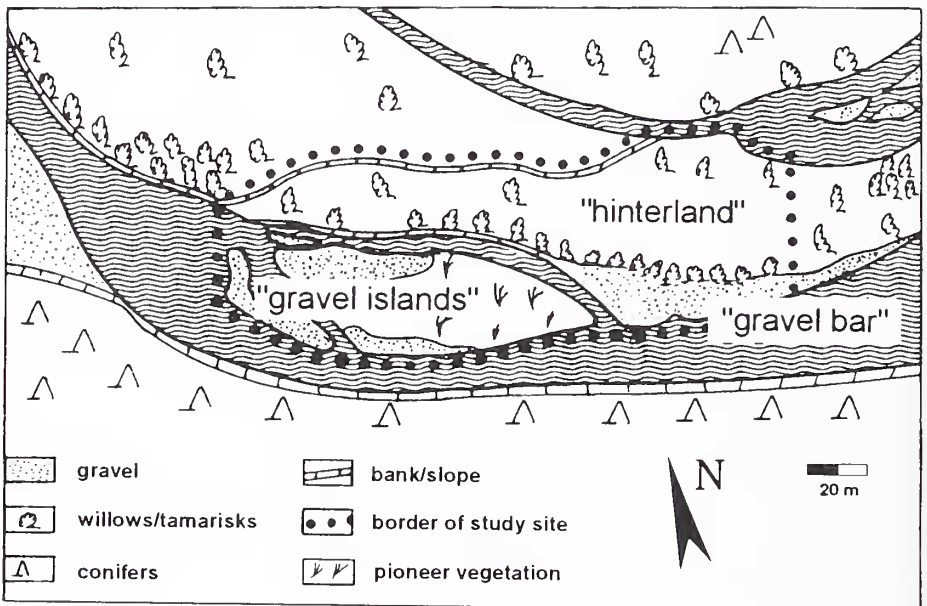

FIG. 1

Study area at the Upper Isar.

1919, up to 25 m^3 s^{-1} of the Isar water has been diverted into the Walchensee to produce hydroelectric power. However, flood events with peak flows of up to 160 m^3-s^{-1} still occur regularly (Bayerisches Landesamt für Wasserwirtschaft, 1988).

The study site, located 820 m above sea level at river-km 242,2, can be distinguished into three parts according to vegetation structure and isolation:

- The "gravel bar" (750 m^2), bare of vegetation.
- The "gravel islands" (2.850 m^2), characterized by an early successional community on sandy substrate dominated by *Calamagrostis pseudophargmites* (Poaceae), *Rinanthus glacialis* (Scrophulariaceae) and willow (*Salix eleagnos*). Willow cover was partly dense in the eastern section of the largest island while the western parts including two smaller islands lacked any vegetation.
- The "hinterland" (5.600 m^2), covered by a later successional community dominated by willows (*Salix eleagnos, S. purpurea*) and the German tamarisk (*Myricaria germanica*). The ground layer was mainly covered by mountain aven (*Dryas octopetala*) and thyme (*Thymus serpyllum*). The vegetation covered 30 - 50%.

The whole study area was devided into grids of 5 x 5 m marked by wooden pegs. Each point where a spider was found, was determined with a precision of about 1 m. The grids also allowed to draw a precise map of substrate structure and vegetation in order to analyse the habitat qualities favoured by the spiders.

Habitat structure

Sediment was categorised into 5 classes according to the relative cover of rocks ($\varnothing$> 20 mm) and fine sediment ($\varnothing$< 2 mm). Two categories were to be found in two different conditions depending on their firmness (table 1). The larger parts of the sediment fraction produce hollows were the night active *A. cinerea* hides during the day.

TABLE 1

Categories of sediment structure

sediment category	cover [%] of stones larger than 20 mm in diameter	main characteristics
1	100	large amount of hollows and crevices, no sandy substrate (no ability to retain moisture)
2	31-99	gaps are filled with sandy substrate
3.f	6-30	firm condition: stones can not be picked up without resistance
3.l	6-30	loose condition: stones can be picked up without resistance
4.f	1-5	firm condition
4.l	1-5	loose condition
5	0	sand only

Six categories were defined in terms of vegetation cover 0%, 1 - 5 %, 6 - 15 %, 16 - 30%, 31 - 60% and 61 - 100%. A higher resolution was used as vegetation became sparse, because *A. cinerea* is especially known for habitats with little vegetation cover.

One of the above categories for sediment structure and vegetation cover was assigned to every m² of the "gravel bar" and the "gravel islands". In order to analyse the preferences of *A. cinerea* with respect to a certain category, the number of captures within each category was compared to the relative share of this category in the whole area. The preference for sediment structure was examined separately, both for spiders on the surface (walking or hiding under stones) and for those within a burrow.

Individual markings and sampling method

To estimate abundance and to assess movement patterns, adults spiders were individually marked with bee tags glued onto their prosoma using a cyane-acrylate based adhesive. In addition, older juveniles with a prosoma width of more than 4 mm (approx. last two juvenile instars) were individually marked with a xylene and toluene free paint. Different colours were applied to the prosoma and one leg segment according to a predetermined code.

Between June 15th and October 12th, 1994 the "gravel islands" and the "gravel bar" were sampled at weekly intervals. Starting in August the "hinterland" was also examined weekly to find those spiders which had retreated from the bank to hibernate in burrows. In 1995 the whole study site was checked on June 15th and July 15th.

In order to prevent a spider leaving the grid without being counted, each 5 x 5 m grid was examined by walking in a spiral from the outer to the inner part. Rocks were turned, small gravel and sandy substrate was combed with the fingers. Burrows were easy to locate either as an open hole or as a small, "hill" of sand, if shut.

Abundance home range and activity

The Jolly index was used to estimate the abundances of *A. cinerea* for each day of the investigation (JOLLY 1965). This allowed for the determination of changes in population density caused by death, birth, immigration and emigration.

Home ranges were determined by connecting the outermost capture points. The area of the resulting polygon is an estimate for the home range of each individual ("minimum area method") (ODUM & KUENZLER 1955, SOUTHWOOD 1979). In contrast to KUENZLER (1958) who considered only those individuals caught at least four times, all individuals captured three or more times were included in the home range estimates of *A. cinerea*.

The activity of different individuals was compared by the "average daily distances" (ADD) measure. ADDs were calculated separately for the whole study period and for three week intervals.

RESULTS

Overall, 393 adult spiders were marked in summer 1994. The recapture rate was 82%. The maximum number of recaptures was 10. On the average, every spider

was captured 4,6 times. Winter mortality appeared to be high. While 119 marked spiders were collected in the study area in October 1994, only six of those were still found in June of the following year. In July 1995 only 5 nymphs and no adult spiders were recorded (fig. 2).
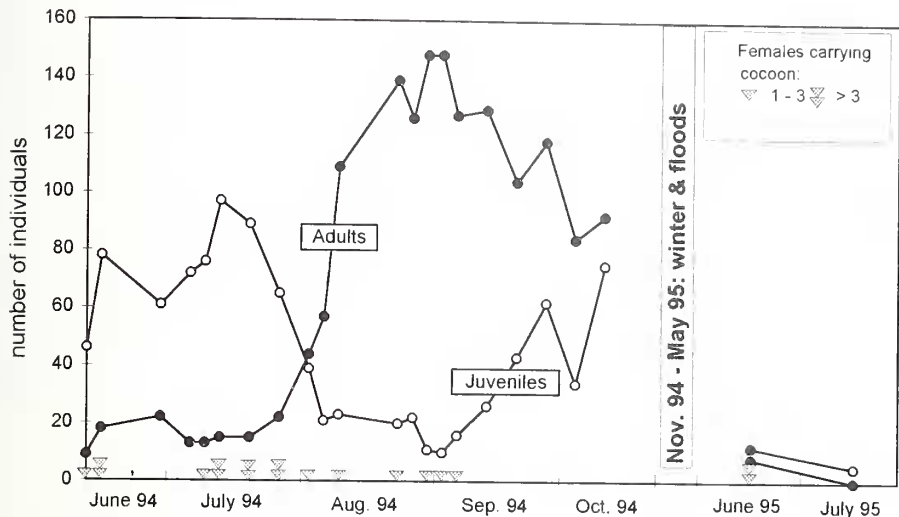

FIG. 2

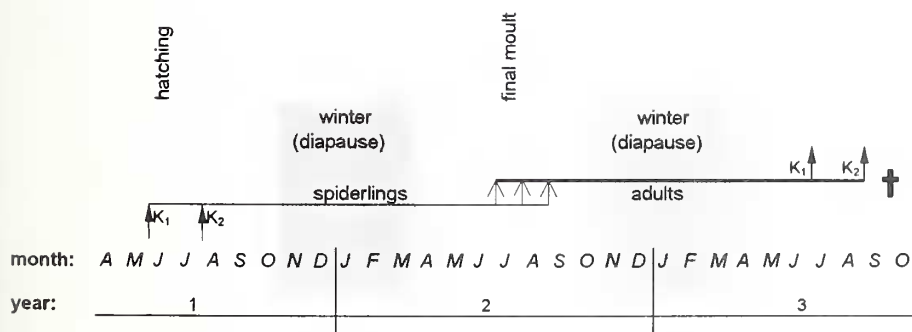Number of spiders caught during the study

FIG. 3

Life cycle of *Arctosa cinerea*
Females carrying a cocoon are indicated by K_1, K_2.

Life cycle and sex-ratio

A cinerea has a two year life cycle (fig. 3). Cocoons are carried by females in June and July/August. The hatched nymphs hibernate in different stages. Their final moult is in August of the following year. Male spiders reach maturity about one week earlier than females. The adults hibernate again. Females then breed in two clearly separated periods in June and from mid July to early August. As an exception to this rule, one female was found breeding from August 22nd to September 7th, 1994 (fig. 2). Only one of 17 females was found to breed in both periods. Since there are always two overlapping generations in a population, adult spiders are found throughout the whole year. The average life span was 41 days for both, adult males and females. The maximum observed life span for an adult female was 314 days. One male survived at least 297 days.

The sex ratio of adult *A. cinerea* is female biased, and constant from early September until the end of the year (♂♂/♀♀ 1:1,8). In the last juvenile instars 113 out of 454 individually marked juveniles were males, 178 females (♂♂/♀♀ 1 : 1,57). The sex of 163 of these nymphs was indeterminable. The surplus of female adults increases after hibernation because males die after mating, whereas the females care for their brood.

Habitat selection and abundance

At the Isar *A. cinerea* prefers vegetation free habitats. As soon as there is a sparse plant cover the number of spiders decreases (fig. 4*a*).
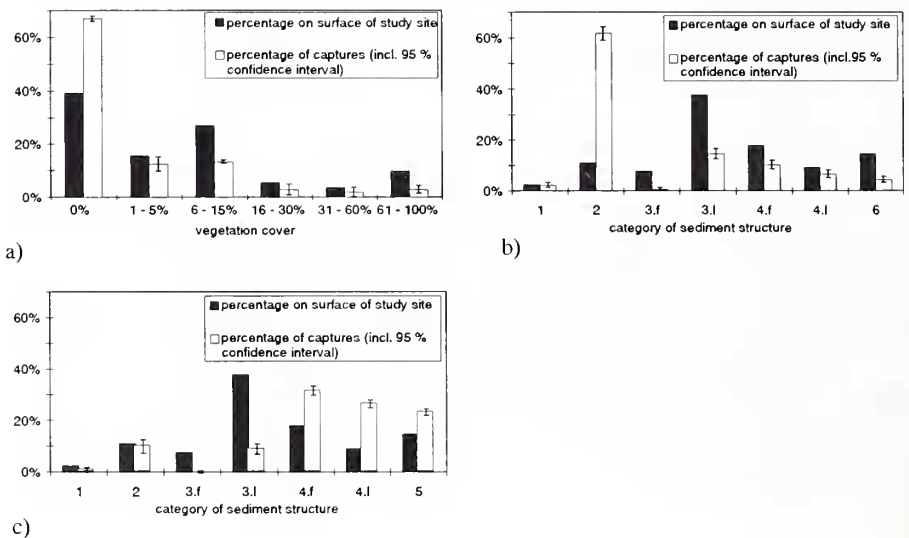

a)

b)

c)

Fig. 4

Habitat association of *Arctosa cinerea* at the study site: (a) captures relative to vegetation cover; (b) captures of vagrant spiders relative to sediment structure (for explanation of sediment categories see table 1); (c) captures in burrows relative to sediment structure

The demands with respect to sediment structure are more complex. After their last moult in August the adult spiders live as vagabonds for about four weeks and then begin to dig a tube. The spiders hibernate in these burrows. Whereas the females remain in their burrows after hibernation, the males wander around. Different sediment types are preferred during the vagrant and the burrowing stages.

Throughout the vagrant period, a clear preference for sediments with a high percentage of stones and rocks (category 2) is obvious, whereas those sediments consisting of smaller particles (3.f, 3.l, 4.f and 5) are avoided (fig. 4b). The vagrant spiders spend the day under rocks without digging burrows. Only occasionally, a small hole dug by the spider can be observed under a rock (7% of all observations). Some spiders were found running on the surface (20%). The same spider was never caught twice under the same rock.

Spiders in burrows show a different distribution. More burrows were found in areas with substrates consisting of smaller pieces (categories 3.l, 4.f, 5) (fig. 4c). In some cases spiders moved between burrows. About 10% of the burrows were not exclusively used by one spider, but rather by several individuals over the sampling period.
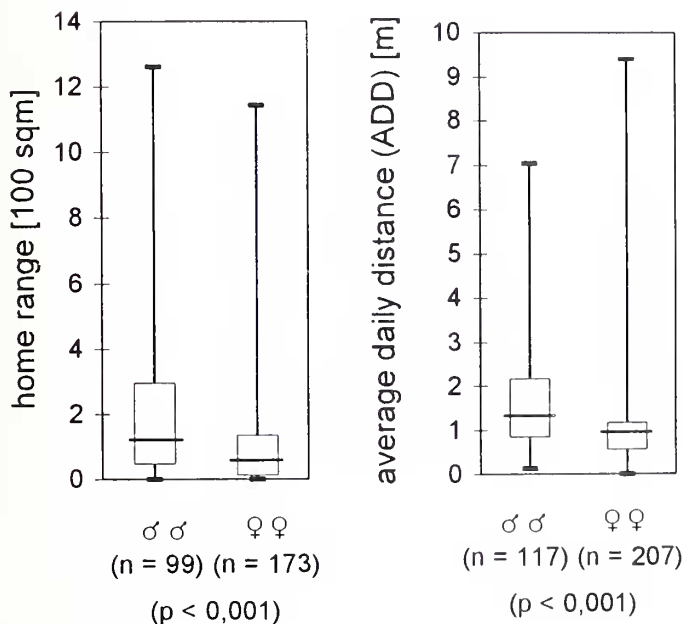

Fig. 5

(a) Home range sizes and (b) average daily distances (ADDs) of *Arctosa cinerea* (median, 1st and 3rd quartile and range between maximum and minimum). Significance of differences between ♀ ♀ and ♂ ♂ is indicated (U-test).

Over the whole study site maximum abundance was 0.03 ind./m² (September 19th, 1994), while by early October the population declined to 0.014 ind./m². The decrease from 269 to 133 individuals within this period corresponds to an average mortality of 5.4 ind./day.

If only the most favoured habitat structures are considered, abundances increase to 0.3 ind./m² (areas with sediment category 2) and 0.13 in./m² (vegetation free areas).

Locomotory activity and home range

Significantly larger home range of males (average: 210 m², maximum: 1.260 m²) than those of females (average: 130 m², maximum: 1.140 m²) indicate a higher mobility of male spiders (fig. 5a). Some spiders remained in the same burrow during the entire observation period (home range regarded as 0 m²).

One single marked male was found on an isolated gravel bank 2 km downstream from the study area after floods in May and June 1995. It was not included in the estimation of home rangesize. However, this recapture shows the potential for dispersal through floods.

While the maximum average daily distance (ADD) was recorded for a female, the average ADD is larger for males (fig. 5b). Lower female activity in July as a result of brood care and higher male activity during a reproduction period in late August/early September account for the significant differences in the ADDs between males and females during these two periods (fig. 6). In October, most spiders have moved into a burrow and only few individuals remained active. The spiders mainly moved east- and northwards leaving the areas near the water edge (FRAMENAU *et al.* 1996).
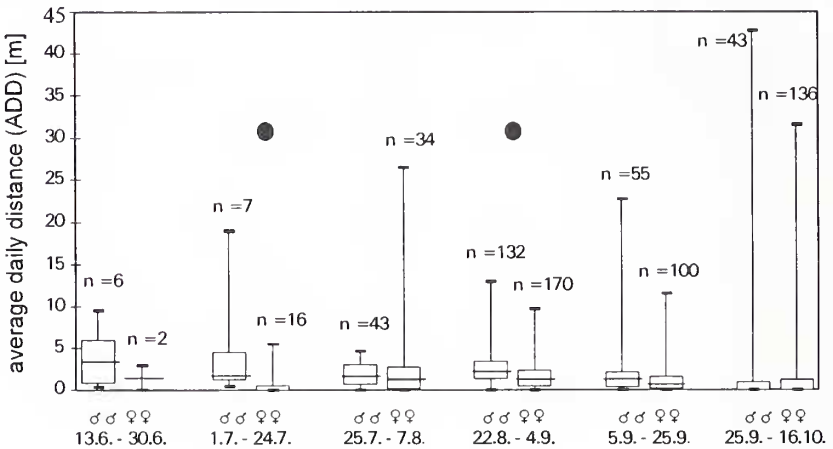

Fig. 6

Average daily distances (ADDs) covered during three week sampling periods in 1994 (median, 1st and 3rd quartile and range between maximum and minimum). ● indicates significant differences between ♀ ♀ and ♂ ♂ (U-test, p < 0.001).

DISCUSSION

Life cycle, phenology and sex-ratio

The exact life cycle is known for only a few sider species (FOELIX 1992). For wolf spiders, life cycles of up to four years have been described (e.g. CONLEY 1985). Smaller lycosid spiders inhabiting gravel bars (e.g., *Pardosa wagleri* (Hahn), *Pirata knorri* (Scopoli)) have a one year life cycle (Framenau, unpublished data). However, the life cycles of spiders are not necessarily correlated to body size only (SCHAEFER 1976). Climatic factors also can play a major role. *Pardosa lugubris* (Walckenaer) hibernates two winters in Sweden and Scotland, but only one in England and the Netherlands (EDGAR 1971):

The two year life cycle of *A. cinerea* corresponds to those recorded for other *Arctosa* species and larger lycosids in Central Europe. *Arctosa perita* (Latreille) needs two years to complete its life cycle (SCHAEFER 1976) just like all *Trochosa* species in central Europe (ENGELHARDT 1964). The two breeding periods in combination with a reproductive activity of males in fall can be explained by a diplochromous activity with two reproductive phases in autumn and in spring. Females copulating in fall breed in June of the following year, while those mating in spring breed in July/August.

Diplochronous activity is recorded only for a few spider species. Just 9 (=3,2%) out of 277 species analysed by Schaefer (1976) for the temperate zone fall into this category. The origin of the diplochronous activity is discussed in detail in TRETZEL (1954), HEYDEMANN (1960), ENGELHARDT (1964) and SCHAEFER (1976).

SCHAEFER (1976) also described diplochrony for *A. cinerea*. However, his results, based on pitfall collections from the coast of the Baltic Sea, differ somewhat from those in the continental alpine region. Along the shores of the Baltic Sea females carrying a cocoon were already found in May, whereas at the Isar they did not appear before June. In June and July Schaefer detected juveniles only. Adults were again found in August and September, which is in accord with the data from the Upper Isar. At this time the males of the new generation show their reproductive activity. In October no spiders were caught along the Baltic Sea.

In coastal and riparian habitats diplochrony can be interpreted as a risk spreading strategy: With one part of the reproductive period in autumn it is guaranteed that there will always be some inseminated females present in spring. Should a flood prevent reproductive activity in spring, these females can be the founders of the next generation.

Female biased sex ratios are well known for social spiders, e.g. the thomisid *Diaea socialis* Main (ROWELL & MAIN 1992) or the ridiid *Anelosimus eximius* (Keyserling) (AVILÉS & MADDISON 1991). However, compared to findings in non-social spiders (HEYDEMANN 1962, HUMPHREYS 1988), the female biased sex ratio of *A. cinerea* is surprising. SCHAEFER (1987) explains female biased sex ratios within spider populations by a shorter lifespan of male spiders. But this does not explain the female biased ratios in the last larval stages recorded for *A. cinerea* along the Upper Isar.

Habitat selection

The preference of *A. cinerea* for vegetation free habitats confirms observations by other authors (e.g. BOCHMANN 1942, KNÜLLE 1953, 1959). In effect, most *Arctosa*

species are known from vegetation free habitats, in particular seashores and river-banks (KNÜLLE 1959, DONDALE & REDNER 1983, TANAKA 1991). Some occupy heath and lichen habitats in high mountains or arctic tundra (DONDALE & REDNER 1983).

A. cinerea depends at least on two different kinds of sediment structure. Banks covered with large gravel offer many hiding places for the vagrant stages and crevices under rocks serve as a shelter against the sunlight, reduce temperature fluctuations and protect *A. cinerea* against predators (e.g. the pompilid wasps *Anoplius infuscatus* and *A. concinnus* (Framenau, unpublished data)). During the burrowing stage *A. cinerea* prefers sandy substrates. The sand enables the establishment of burrows.

Presumably due to its large size, the density of *A. cinerea*, even in the most preferred microhabitats (0,3 Ind./m^2) is low compared to about 3 ind./m^2 for *Trochosa ruricola* (De Geer) (HACKMAN 1957) and 1,4 ind./m^2 for *Pardosa agricola* (Thorell) (ALBERT & ALBERT 1976). The habitat association of *A. cinerea* shows that this species strictly depends on the dynamics of the river. Floods, on one hand cause high mortality, on the other hand they guarantee the existence of vegetation free gravel bars and sandy areas which otherwise would soon fall into succession (MÜLLER 1991).

Locomotory activity and home range size

Locomotory activity in wolf spiders mainly reflects the search for suitable microhabitats and sexual activity (CADY 1984; ENDERS 1975). KUENZLER (1958) found home ranges for lycosids to be smaller than those recorded for *A. cinerea*. The average home range size of *Hogna timuqua* (Wallace) is 41,7 m^2 for males and 9,6 m^2 for females.

Large home range sizes in *A. cinerea* are mainly caused by movements in autumn. The spiders retreat from the water edge before hibernation. This can be interpreted as a search for a more protected area for the winter diapause (FRAMENAU *et al.* 1996).

REFERENCES

ALBERT, A.M. & ALBERT, R. 1976. Abundance and biomass of *Pardosa agricola* (Thorell) (Araneae, Lycosidae) on a shingle bank of the River Lune (Lancashire). *Bulletin of the British Arachnological Society* 3 (9): 237-242.

AVILÉS, L. & MADDISON, W.P. 1991. When is the sex ratio biased in social spiders? Chromosome studies of embryos and male meiosis in *Anelosimus* species (Araneae: Theridiidae). *Journal of Arachnology* 19: 136-145.

BAYERISCHES LANDESAMT FÜR WASSERWIRTSCHAFT (ed.). 1988. Deutsches Gewässerkundliches Jahrbuch Donaugebiet. Abflußjahr 1987, *Munich*, 248 pp.

BIGOT, L. & FAVET, C. 1985. La communauté ripicole des araignées de la basse Durance. *Bulletin de la Société Linnéenne de Provence* 37: 53-68.

BOCHMANN, G. v. 1942. Die Spinnenfauna der Strandhaferdünen an den deutschen Küsten. *Kieler Meeresforschungen* 4 (1): 38-69.

BOUMEZZOUGH, A. 1983. Les communautés animales ripicoles du bassin versant de la rivière Aille (Var - France), II: Composition et structure de la faune épigée. *Ecologie Mediterranée* 9 (2): 3-56.

CADY, A.B. 1984. Microhabitat selection and locomotor activity of *Schizocosa ocreata* (Walckenaer) (Araneae: Lydcosidae). *Journal of Arachnology* 11: 297-307.

CONLEY, M.R. 1985. Predation versus resource limitation in survival of adult burrowing wolf spiders (Araneae: Lycosidae). *Oecologia, Berlin* 67: 71-75.

DONDALE, C.D. & REDNER, J.H. 1983. Revision of the wolf spiders of the genus *Arctosa* C.L. Koch in North and Central America(Araneae: Lycosidae). *Journal of Arachnology* 11: 1-30.

DRÖSCHMEISTER, R. 1994. Die Spinnenfauna der Kies- und Schotterbänke des nordalpinen Wildbaches Halblech (Landkreis Ostallgäu). *Berichte des Naturwissenschaftlichen Vereins Schwaben* 98 (3): 61-70.

EDGAR, W.D. 1971. Seasonal weight changes, age structure, natality and mortality in the wolf spider *Pardosa lugubris* Walck in Central Scotland. *Oikos* 22: 84-92.

ENDERS, F. 1975. The influence of hunting manner on prey size, particularly in spiders with long attack distances. - *American Naturalist* 109: 732-763.

ENGELHARDT, W. 1964. Die mitteleuropäischen Arten der Gattung *Trochosa* C.L. Koch, 1848 (Araneae, Lycosidae). Morphologie, Chemotaxonomie, Biologie, Autökologie. *Zeitschrift für Morphologie und Ökologie der Tiere* 54: 219-392.

EWENS, W.J., BROCKWELL, P.J. GANI, J.M. & RESNICK, S.I. 1987. Minimum viable population size in the presence of catastrophes, pp. 59-68. *In:* Viable Populations for Conservation (M.E. SOULÉ, ed.). *Cambridge University Press, Cambridge*, 189 pp.

FOELIX, R.F. 1992. Biologie der Spinnen, *Thieme, Stuttgart*, 331 pp.

FRAMENAU, V., REICH, M. & PLACHTER, H. 1996. Zum Wanderverhalten und zur Nahrungsökologie von *Arctosa cinerea* (Fabricius, 1777) (Araneae: Lycosidae) in einer alpinen Wildflußlandschaft. *Verhandlungen der Gesellschaft für Ökologie, Freising-Weihenstephen,* 25: in press.

HACKMAN, W. 1957. Studies on the ecology of the wolf spider *Trochosa ruricola* Deg. *Commentationes Biologicae* 16 (6): 1-34.

HERING, D. 1996. Nahrung und Nahrungskonkurrenz von Laufkäfern und Ameisen in einer nordalpinen Wildflußaue. *Archiv für Hydrobiologie, Supplement,* 111 (Large Rivers 9), in press.

HEYDEMANN, B. 1960. Die biozönotische Entwicklung vom Vorland zum Koog. I. Teil: Spinnen (Araneae). *Abhandlungen der mathematisch-naturwissenschaftlichen Klasse. Akademie der Wissenschaften und der Literatur, Mainz,* 11: 745-913.

HEYDEMANN, B. 1962. Untersuchungen über die Aktivitäts- und Besiedelungsdichte bei epigäischen Spinnen. - *Verhandlungen der Deutschen Zoologischen Gesellschaft* 25: 538-556.

HOVESTADT, T., ROESER, J. & MÜHLENBERG, M. 1991. Flächenbedarf von Tierpopulationen. *Berichte aus der Ökologischen Forschung* 4: 435 pp.

HUMPHREYS, W.F. 1988. The ecology of spiders with special reference to Australia. Australian Arachnology. *Australian Entomological Miscellaneous Publication* 5: 1-22.

JOLLY, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration - stochastic model, *Biometrika* 52: 225-247.

KNÜLLE, W. 1953. Zur Ökologie der Spinnen an Ufern und Küsten. *Zeitschrift für Morphologie und Ökologie der Tiere* 42: 117-158.

KNÜLLE, W. 1959. Über italienische Arctosa-Arten (Araneae: Lycosidae). *Archivio Zoologico Italiano* 44: 251-270.

KUENZLER, E.J. 1958. Niche relations of three species of lycosid spiders. *Ecology* 39 (3): 494-500.

KUHNELT, W. 1943. Die litorale Landtierwelt ostalpiner Gewässer. *Internationale Revue der gesamten Hydrobiologie* 43: 430-457.

LUKEN, J.O. 1990. Directing ecological succession, *Chapman and Hall, London*, 251 pp.

MANDERBACH, R. & REICH, M. 1996. Auswirkungen großer Querbauwerke auf die Laufkäferzönosen von Umlagerungsstrecken der Oberen Isar - *Archiv für Hydrobiologie Supplement, 111 (Large Rivers 9)*, in press.

MÜLLER, N. 1991. Auenvegetation des Lech bei Augsburg und ihre Veränderungen infolge von Flußbaumaßnahmen. *Augsburger Ökologische Schriften* 2: 79-108.

ODUM, E.P. & KUENZLER, E.J. 1955. Measurement of territory and home range size in birds. *Auk* 72: 128-137.

PLACHTER, H. 1986a. Die Fauna der Kies- und Schotterbänke dealpiner Flüsse und Empfehlungen für ihren Schutz. *Berichte der Akademie für Naturschutz und Landschaftspflege* 10: 119-147.

PLACHTER, H. 1986b. Composition of the carabid beetle fauna of natural riverbanks and of Man-made secondary habitats, pp. 509-335. *In:* Carabid Beetles. Their adaptations and dynamics (P.J. denBOER, M.L. LUFF, D. MOSSAKOWSKI & F. WEBER, eds). *Gustav Fischer, Stuttgart/New York*, 551 pp.

PLATNICK, N.I. 1993. Advances in Spider Taxonomy 1988-1991. With Synonymies and Transfers 1940-1980. *New York Entomological Society in association with The American Museum of Natural History.* 846 pp.

REICE, S.R. 1994. Non equilibrium determinants of biological community structure. *American Scientist* 82: 424-435.

ROWELL, D.M. & MAIN, B.Y. 1992. Sex ratio in the social spider Diaea socialis (Araneae: Thomisidae). *Journal of Arachnology* 20: 200-206.

SACHER, P. 1992. Rote Liste der Spinnen Brandenburgs, pp. 220-234. *In:* Gefährdete Tiere Brandenburgs (Rote Liste). *Ministerium für Umwelt, Naturschutz und Raumordnung des Landes Brandenburg (Selbstverlag), Potsdam*, 288 pp.

SCHAEFER, M. 1976. Experimentelle Untersuchungen zum Jahreszyklus und zur Überwinterung von Spinnen (Araneida). *Zoologische Jahrbücher, Abteilung für Systematik, Oekologie und Geographie der Tiere* 103: 127-289.

SCHAEFER, M. 1987. Life Cycles and Diapause, pp. 331-347. *In:* Ecophysiology of Spiders (W. NENTWIG, ed.). *Springer, Berlin*, 448 pp.

SHAFFER, M. 1987. Minimum viable populations: coping with uncertainty, pp. 69-86. *In:* Viable Populations for Conservation (M.E. SOULÉ, ed.). *Cambridge University Press, Cambridge*, 189 pp.

SOUTHWOOD, T.R.E. 1979. Ecological Methods. *Chapman and Hall, London*, 391 pp.

TANAKA, H. 1991. Lycosid spiders of Japan VII. The genus *Arctosa* C.L. Koch. *Sonoda Women's College Studies* 25: 289-316.

TRETZEL, E. 1954. Reife- und Fortpflanzungszeit bei Spinnen. *Zeitschrift für Morphologie und Ökologie der Tiere* 42: 634-691.